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ON THE ABDOMINAL STRUCTURE OF CERTAIN BEETLE LARVÆ OF THE CAMPODEIFORM TYPE. A STUDY OF THE RELATION BETWEEN THE STRUCTURE OF THE INTEGUMENT AND THE MUSCLES.¹

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Doctor Hopkins' classical monograph of the genus *Dendroctonus*, 1909,² was the first successful attempt to formulate a complete and practical terminology for the external structure of a Coleopterous larva, and may well serve, as Doctor Hopkins expressed it in his introduction, "as a guide to the determination of further facts relating to insect anatomy in general." The need of such a uniform terminology for the Coleopterous larva as elaborated by Doctor Hopkins in this monograph, had long been felt, because a truly comparative description is not possible without a defined terminology comprising *all* the body parts. The descriptions of even Schiödte, the unsurpassed master of larval classification, are lacking in this respect. The work of Doctor Hopkins was readily appreciated by students of the subject. Thus Henriksen³ Kemner⁴ Rosenberg,⁵ and the writer⁶ have at once adopted his terminology in so far as it was found applicable to the so-called compodeiform larval type with which these authors worked. The external skeleton of the abdominal parts of this campodei-

¹ Contribution from Division of Forest Insect Investigations. Bur. of Ent., U. S. Dept. of Agric.

² Hopkins, A. D., The genus *Dendroctonus*. (U. S. Dept. Agric., Bur. of Ent., Tech. Ser. no. 17. Part I, Washington, D. C., 1909, pp. 57-64.)

³ Henriksen, Kaj L., Danske Elateridelarver, Entomologiske Meddelelser, II ser., vol. iv, 1911, pp. 225-331. Idem, Pragtbiller og Smeldere "Danmarks Fauna," published by Dansk Naturhistorisk Forening, 1913.

⁴ Kemner, A. Beitrage zur Kenntniss einiger Schwedischen Koleopterenlarven, Arkiv für Zoologie, Bd. 7, no. 31, 1912, p. 1-31.

⁵ Rosenberg, E. C., Bidrag til Kundskaben om Billernes Levevis, Udvikling og Systematik. III, Billefauna i Dyrboer, Entomologiske Meddelelser, vol. 10, 1913, pp. 37-76.

⁶ Böving, Adam, Nye Bidrag til Carabernes Udviklingshistorie I Entomologiske Meddelelser, II ser., vol. III, 1910, pp. 219-376. Idem, Nye Bidrag til Carabernes Udviklingshistorie, II. Entomologiske Meddelelser II, ser. vol. iv, 1911, pp. 129-180.

form type differs, however, from that of the Scolytidæ with which Doctor Hopkins dealt, and his terminology elaborated for the Scolytidæ is therefore not immediately applicable to the campodeiform larvæ. In the hope of finding a foundation for a natural and logical terminology for the body of this type, I began, some years ago, a detailed study both of the external and internal surfaces of the skin as well as of the arrangement of the muscles in these larvæ. I have been fortunate in being able to continue these studies under most favorable conditions since my arrival in this country. In Denmark, I studied more particularly the Carabid, Dytiscid and Hydrophilid larvæ, while here the Trogositid, Clerid and Elaterid larvæ were chosen, because they play a more important rôle in the Branch of Forest Insects, with which I became connected.

Some of the results of these studies are presented in this paper, and I believe they will be found useful in the study of other campodeiform larvæ. The eventual application of these results also to the deviating eruciform type to which the Scolytidæ belong, I purposely postpone. I believe that the characters of these two groups eventually may be homologized, but this will involve considerable further anatomical study and the question is not taken up in this paper. From the insufficient investigations I have made of Lepidopterous, Hymenopterous and Neuropterous larvæ, I am inclined to believe that the characters described in the present paper will be found useful in the larval study of all the insects with complete metamorphosis.

While the terminology has been derived from an anatomical study of the inside of the integuments and of the muscles, the structures can also be made out externally, but they can only be understood by a study of the inside, and it would have been impossible to homologize the external characters without a comparative study of the muscles. It should be stated however that the terms used in this paper for the various structural parts are purely provisional. The limitation and definition of the areas has been the main object; the names have been a minor consideration.

THE INTERSEGMENTAL SKIN

The segments of an insect larva are, as is well known, connected by a perpendicular intersegmental skin, but a more intimate study of this skin has never been made. This intersegmental skin is divided on each side into two more or less wedge-shaped parts: the superior cunea (*s*) with the point downwards, and the inferior cunea (*i*) with the point upwards. The ends of these two cuneæ pass each other more or less, that of the superior cunea always

in front of the inferior. At the end of each cunea there is a thickening of the membrane which on the inside forms a small notch to which muscles are attached. I call these thickenings relatively, the anterior (*an*) and the posterior (*pn*) cuneal notch. Another similar notch is found in the upper portion of the anterior cunea; I call this the superior cuneal notch (*sn*). Finally there is a fourth notch on the median ventral line of the posterior cunea; this I term the ventral cuneal notch (*vn*).

THE LATERAL ZONE

Between the posterior cuneal notch of one intersegmental skin and the anterior cuneal notch of the succeeding intersegmental skin is found, on the inside of the integument, a staff-like or even carinated apodeme, which on the outside appears as a deep groove. This groove has been named by Doctor Hopkins the pleural suture (*pl*). Above and parallel with the pleural suture is found a similar one which I call the antipleural suture (*anti*). This is sometimes more, sometimes less developed than the pleural suture. It is somewhat shorter than the pleural suture and does not reach either of the margins of the segment. The bandlike region between these two sutures I call the lateral zone. This lateral zone has, as already pointed out by Dr. David Sharp in his handbook, 1901, p. 90, a mechanical use in the dorso-ventral compression of the larval body corresponding to that of the intersegmental skin in the telescoping compression, and it is stiffened on the inside by a circular thickening which touches both the antipleural and the pleural suture. This circular thickening limits an area, which on the outside is elevated and rounded; it is the area which has been termed the pleural lobe (*pll*) by Doctor Hopkins. The rest of the lateral zone is divided by oblique sutures into four small triangular parts, two before, and two behind the pleural lobe. I call these respectively the protopleurite (*prpl*), the deutero-pleurite (*dpl*), the tritopleurite (*tripl*) and the tetrapleurite (*tetpl*). All of these four small areas are prolonged more or less upward along the superior cunea.

The whole lateral zone can be compressed by two systems of perpendicular muscles. The muscles of the first system run upwards from the middle of the pleural suture; while the muscles of the other system run downward from each end of the antipleural suture. When the muscles are relaxed, the pleural and antipleural sutures are again separated by the elasticity of the pleural lobe and of the oblique sutures.

THE DETERMINATION OF THE LINES AND AREAS ABOVE AND BELOW
THE LATERAL ZONE

Above the antipleural suture the segment is divided into the following areas:

Prescutum (*prsc*), scutum (*sc*), scutellum (*scl*), parascutum (*pasc*), postscutellum (*pscl*), and the spiracular area (*spa*).

The scutum and scutellum, which are sometimes hardly separable, form the central dorsal part; in front of these is the prescutum, below and partly around them the parascutum, and behind them, the postscutellum. Underneath those areas and limited on the other side by the antipleural suture lies the spiracular area.

All areas are defined by lines, fine wrinkles in the integument, radiating from and determined by muscle attachments. In order to make the figures as comprehensible as possible and in order to avoid too many letters I have signified the muscle spot, its radiating lines, and the area determined thereby, by the same letter, and each muscle is then determined by the letters of the two muscle spots between which it runs. The boundary line of scutum and scutellum, I call the scutal line (*sc*). This is determined by a muscle spot from which a long muscle (*sc-pn*) runs down to the posterior cuneal notch. The transversal line separating scutum and scutellum I call the scuto-scutellar line. The prescutum is bounded by a line, the prescutal line (*prsc*), which runs from the superior cuneal notch to the anterior margin of scutum. The boundary line of parascutum, I call the parascutal line (*pasc*). This is determined by a bundle of three muscles (*pasc-pl*), which run down to the pleural suture (*pl*). The parascutum is divided by a more or less curved line connecting the scutal and the parascutal line. I call this line the parascutal divisor (*d*). It is determined by a flat muscle band (*d-s*), which runs backwards to the superior cunea (*s*). This line is in reality a row of little dots and varies considerably in size and position in the different types of larvae; often it is also continued downward, below the parascutal line. The postscutellum (*pscl*) is limited by the postscutellar line, which runs behind the parascutum through the superior attachment of the muscle (*pscl-hypl*), and terminates at the posterior end of the antipleural suture. The spiracular area (*spa*), is characterized by the presence of the spiracle and is limited above by the parascutal line, below by the antipleural suture.

AREAS BELOW THE LATERAL ZONE

Below the pleural suture the segment is separated into the following areas: the hypopleurite (*hypl*) immediately below the pleural suture, the presternum (*prst*) and sternum (*st*), generally

more or less united, separated by the triangular parasternum (*past*), from the sternellum (*stl*), behind which is the poststernellum (*pstl*).

The line limiting the hypopleurite below, I call the hypopleural line (*hypl*) and it is determined by perpendicular muscles running from the posterior end of the antipleural suture (*anti-hypl*). This hypopleural line consists of two pieces. Below the anterior piece lies the parasternum, below the posterior, the poststernellum. The line separating the parasternum from the sternum I call the sternal line (*st*). This is determined by three long oblique muscles, two from the superior cunea, just in front of the spiracle of the following joint (*s-st*) and one (*an-st*) from the anterior cuneal notch. The two first mentioned muscles are closely united at their lower end in the *Trogosita* and *Alaus* larvæ, while in *Clerus* they are plainly separated (fig. 1, pl. III). The line limiting poststernellum anteriorly against sternellum I call the poststernellar line (*pstl*), and this is determined by a short oblique muscle from the anterior cuneal notch (*an-pstl*). The other, anterior, side of sternellum is defined by a line, the sternellar line (*stl*), from the end of the anterior piece of the hypopleural line to the posterior end of the sternal line.

The study of the muscles, is as stated in the beginning, essential to the correct understanding of these integumental parts. Without such a study it is well nigh impossible to interpret the structure of the surface in the more complicated cases. A few examples will suffice to demonstrate this. In *Alaus* (fig. 8, pl. VI), the muscles show that the first line below the pleural suture is but a branch from the hypopleural line which is normally simple, and that the hypopleurite, consequently, in this larval type consists of two distinct pads, while in the other types this area is undivided. Similarly, it could not have been recognized without muscle study that the broken sternal line in *Trogosita* (fig. 5, pl. V), is identical with the straight sternal line in *Clerus* (fig. 1, pl. IV), and *Alaus*, a modification which makes the shape of the parasternum quite different in these forms.

In the above I have only mentioned the muscles, which have a direct bearing on the formation of the various areas. There are, however, a great many others, and a short account of these may be useful in the identification and location of the leading muscles, used in this paper. They are:

(*s-s*). Longitudinal, bandlike dorsal, muscles in parallel series immediately underneath the integument as far down as to the spiracle; they run between a superior cunea in front and the following superior cunea posteriorly (fig. 3).

(*i-i*). Longitudinal, bandlike, ventral muscles in parallel series

immediately underneath the integument, below the pleural suture; they run between an inferior cunea in front and the following inferior cunea (fig. 3).

(*st-i*). Small oblique muscles between sternum and the inferior cunea (fig. 2).

(*s-fw⁷-sc*). Longitudinal muscles from the superior cunea above the superior cuneal notch, across the scutellum to the scutum.

(*s-fw-scl*). Oblique muscles from the superior cunea to the scutellum (fig. 3).

(*an-tetpl*). An oblique, single, small muscle from the anterior cuneal notch to the superior part of the tetrapleurite (fig. 4).

(*an-sn*). A vertical pair of muscles from the anterior cuneal notch to the superior cuneal notch (fig. 4).

(*an-pn*). A single, horizontal muscle between a posterior cuneal notch and the anterior cuneal notch of the following intersegmental skin (fig. 3).

(*vn-dpl*). One or two large, oblique muscles from the ventral cuneal notch to the anterior curve of the pleural suture below the deuteropleurite (fig. 4).

(*dpl-fw-s*). An oblique, short, but rather broad band from the anterior curve of the pleural suture below the deuteropleurite to the superior cunea near the spiracle (fig. 4).

(*dpl-prst*). A vertical muscle from the anterior curve of the pleural suture below the deuteropleurite to the presternum. (This I have found only in *Trogosita*, fig. 6.)

(*spa-pn*). A pair of perpendicular muscles between the posterior cuneal notch and the spiracular area just below the spiracle.

(*pl-hypl*). One or some few small vertical muscles from the middle of the pleural suture to the hypopleural line (fig. 4, fig. 6, 2. Not found in *Alaus*.)

(*tetpl-hypl*). A vertical muscle from the tetrapleurite to the hypopleural line (fig. 4).

(*pscl-hypl*). A long, perpendicular muscle from postscutellum to the hypopleural line, the definition of the postscutellar line (fig. 2). See p. 58.

In the preceding I have endeavored to demonstrate that the abdomen of the larvæ under consideration is made up, in an identical manner, of the intersegmental skin, the lateral zone, and the regions above and below the lateral zone, and further that the arrangement of the muscles between these parts is uniform. This remarkable uniformity of structure has been preserved throughout the genetic evolution because it enables and conditions the elementary movements of the abdomen. These elementary movements are but two. First, the telescoping of the segments,

⁷ *fw* indicates "forwards to;" *bw* indicates "backwards to."

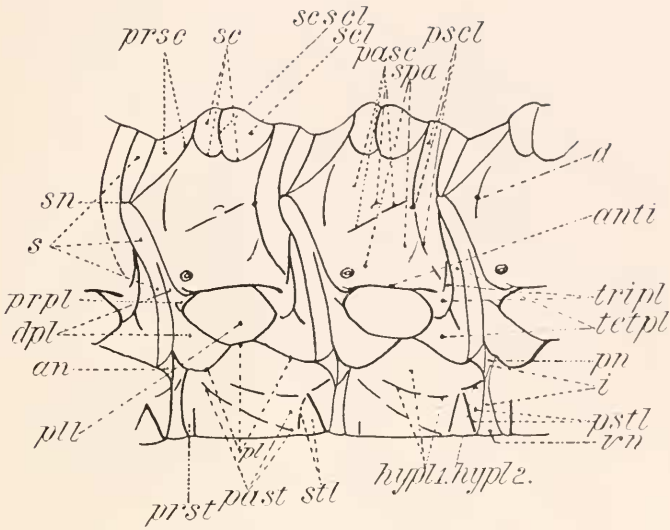


Fig 1. *Clerus* (x 20)
The areas of abdomen

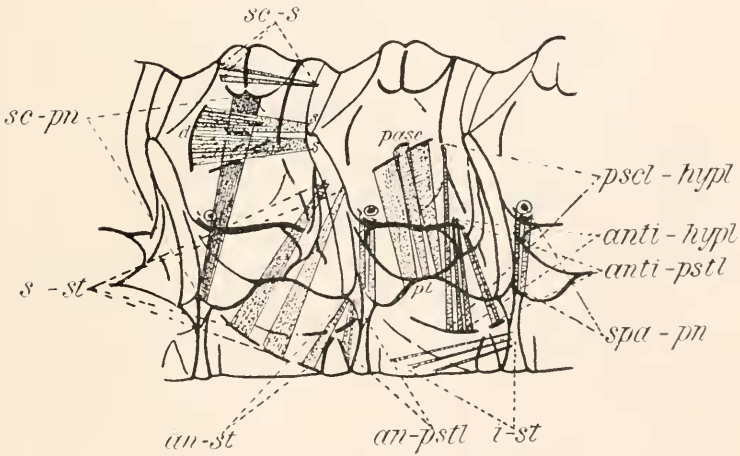


Fig 2. *Clerus* (x 20)
Muscles causing boundary lines of the different areas